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VISUAL ACUITY OF THE SHEET-WEB BUILDING SPIDER *BADUMNA INSIGNIS* (ARANEAE, DESIDAE)

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ABSTRACT. Visual acuity in the sheet-web building spider *Badumna insignis* (L. Koch 1872) (Araneae, Desidae) was examined in relation to its microhabitat. We examined, using histological techniques, the major structural and functional features of the visual systems, including external and internal ocular organizations, resolution, sensitivity, focal lengths and the field of view for each eye. *Badumna insignis* showed little differentiation in its ocular arrangement from the presumed ancestral condition in spiders, with poor visual acuity and a small field of view. Resolution and sensitivity were low, particularly in the secondary eyes. The AM eyes were enhanced showing larger fields of view and higher sensitivity, resembling that of nocturnal uloborids. These eyes appear adapted for close-range recognition, due to short-range focus and good visual overlap.

Keywords: Corneal eye, vision, field of view, sheet-web

Spiders are renowned for their effective and complex visual systems (Land 1985). The primitive eye arrangement of spiders, as hypothesized by Homann (1971), consists of two transverse rows each containing four eyes. The first row consists of the anterior median (AM) eyes in the middle and the anterior lateral (AL) eyes on the periphery. Similarly, the posterior eyes are grouped into posterior median (PM) eyes and posterior lateral (PL) eyes. However, deviations from this pattern are common in extant species. The eyes of spiders often form three or four rows and certain pairs of eyes may become specialized and enlarged, while other pairs may become reduced or lost (Homann 1971; Comstock 1948). The visual capacity of spiders varies according to the size, shape, internal arrangement and position of the visual field of the eyes (Forster 1979; Foelix 1982; Opell & Cushing 1986; Opell & Ware 1987; Land & Barth 1992).

Visual acuity is a combination of many aspects of the visual system such as field of view, focal length, resolution and sensitivity. The external placement and internal arrangement determine the field of view of each eye (Land 1985). Forward-facing binocular vision is a product of overlapping visual fields, and is necessary for good distance judgment. The distance over which an eye can focus upon an object is determined by the focal length of its lens (Homann 1971). This ranges from 38.01 μm in the AL eyes of the uloborid *Hyptiotes cavatus* (Hentz 1847) (although this eye appears to be vestigial; Opell & Ware 1987), to 448 μm in the PM eyes of the ctenid *Cupiennius salei* (Keyserling 1877) (Land & Barth 1992). Sensitivity, or the ability to see in low light levels varies, generally in relation to the light conditions under which each species operates (Opell & Ware 1987). The number of visual cells (rhabdomeres) within the retina determines the quality of image resolution (Foelix 1982). Small numbers of rhabdomeres in the retina, such as 10–20 in some eyes of the ochyroceratid *Speocera* (Berland 1914), detect little more than movement (Homann 1971). In contrast, the PM eyes of the wolf spider *Lycosa tarantula* (Linnaeus 1758), contain about 5470 rhabdomeres and would thus have greater image resolution (Kovoor et al. 1992).

Visual acuity in a spider is often related to the microhabitat that it occupies, or the type of prey and method of capture (Forster 1979; Rovner 1993; Schmid 1998; Ortega-Escobar & Munoz-Cuevas 1999). However, much of the literature is limited to spiders in relatively few microhabitat types, such as salticids, ac-

[1] Deceased.

tively-hunting jumping predators (Land 1969; Forster 1979; Harland & Jackson 2000 2002; Parker & Hegedus 2003); lycosids, ground dwelling sit-and-wait predators (Lizotte & Rovner 1988; Land & Barth 1992; Rovner 1993; Persons & Uetz 1996, 1998; Grusch et al. 1997; Schmid 1998; Ortega-Escobar & Munoz-Cuevas 1999; Dacke et al. 2001); uloborids, orb web or single line web building spiders (Opell & Cushing 1986; Opell & Ware 1987; Opell 1988) and *Deinopis subrufa* (L. Koch 1879), a net casting spider (Blest & Land 1977). Few studies have focused on visual acuity in a sheet-web building spider.

We examined the focal length, resolution, sensitivity and field of view in *Badumna insignis* (Koch 1872), which builds an asymmetrical sheet-web that extends from a tubular retreat and is attached to a substrate. The web consists of many pairs of parallel support lines overlain with zigzag threads of cribellate silk that function to entangle prey (Main 1976; Opell 1999). The sheet-web of *B. insignis* both defines the individual's foraging patch and provides some shelter from predators. Vibrations on the web can also be used to recognize the identity of an object (Suter 1978; Barth 1982; Masters et al. 1986; Herberstein et al. 1998). In natural situations *B. insignis* builds its web under the shelter of logs, loose bark of trees, rocks, cliffs and stones, preferring dry positions (Main 1964). However its opportunistic nature has allowed it to take advantage of areas settled by humans, where it is quite common around houses, sheds, window-sills, under eaves and rafters, boxes and outdoor furniture (Main 2001).

METHODS

Twenty adult female specimens of *Badumna insignis* (L. Koch 1872) were collected over a period of three weeks during February 2001, within the grounds of The University of Western Australia.

External ocular organization.—Three external features were measured on each specimen: total eye width (TEW), total eye depth (TED) and eye diameters (Fig. 1). These measurements may be influenced by both orientation of the lens and the amount of tissue devoted to each eye type. Measurements were taken under a binocular dissecting microscope with an ocular micrometer. Since all the external features correlated significantly with carapace length (with the exception of the diameter of the PM eyes $P = 0.054$), values were standardized for the animals' size by dividing each measurement by the carapace length. Repeated measures ANOVA with one within subject factor and no between subject factors, and Student-Newman-Keuls post-hoc tests, were used to determine significant differences in the relative eye diameters.

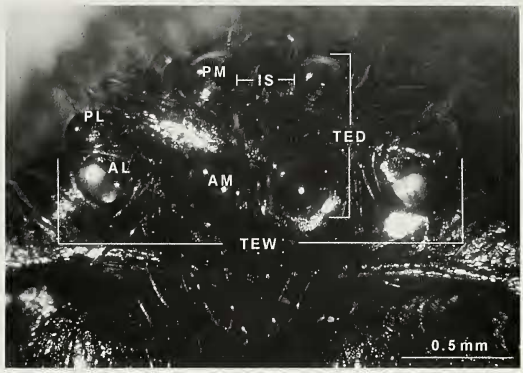


Figure 1.—External measurements taken on *B. insignis*; AM = anterior median eyes; AL = anterior lateral eyes; PM = posterior median eyes; PL = posterior lateral eyes; TED = total eye diameter; TEW = total eye width; IS = interocular space.

Internal ocular organization.—Three specimens of *B. insignis* were killed, using CO_2 gas, and the cephalathorax trimmed to a small block of tissue and fixed in Karnovsky's fixative for 72 hours. Specimens were then washed and further trimmed down in spider saline (scorpion saline excluding the $CaCl_2$; Zwicky 1968) and placed in phosphate buffer prior to being embedded in araldite/procure. Longitudinal and transverse sections (1 μm thick) were cut using an LKB ultratome and a diamond knife. Sections were mounted on slides and stained with toluidine blue. These sections were used to determine the internal ocular organization and to measure resolution, sensitivity and field of view of individual eyes.

Resolution.—The numbers of axons exiting each eye were counted from sections cut using the same methods as for internal ocular organization. Resolution is dependent upon the number of photoreceptors, or rhabdomeric cells per eye. The higher the density of cells the finer the resolution of an image (Land 1985). The number of nerve axons exiting a

spider's eye is in a 1:1 ratio with the number of photoreceptors (Uehara & Uehara 1996).

Focal length.—The focal length of each lens was determined using the 'hanging drop' method described in Homann (1928) and Land (1985). The lens, along with a small proportion of the surrounding cuticle, was dissected from the head and stored in spider saline. After being cleared of excess tissue in warm, dilute sodium hydroxide, the lens was suspended in a drop of spider saline from the underside of a cover slip. Using a microscope, the image through the lens was then viewed, targeting an object of known size (o). The distance between the lens and the object was then measured using callipers (μ). The size of the image (i) was determined, and the focal length was calculated, using the formula described by Opell & Ware (1987: Table 1). For each lens type an average of the values measured was determined. Repeated measures ANOVA, with one within subject factor (eye) and no between subject factors, with a Tukey/Kramer post-hoc test, was used to determine differences between the focal lengths of the different eyes.

Sensitivity.—Sensitivity (*f*-number), or the eye's ability to admit light, was calculated using values for focal length (F) and the diameter of the retina (d), measured from the extremities of the rhabdomeres in each species (Opell & Ware 1987). The resulting *f*-number is inversely related to the eyes ability to admit light (Land 1985). Focal lengths were determined by the above methods and retinal diameters were determined by taking measurements from slides obtained using methods described for internal ocular organization. These values were then entered into the sensitivity equation outlined in Opell & Ware (1987: Table 1).

Field of view.—Histological investigation revealed *B. insignis* has a 'canoe shaped' tapetum, which reflects light at an acute angle making it impossible to determine the field of view using ophthalmoscopy (Land 1985). Therefore, the visual field was determined using physical measurements of the lens and the surrounding retinal hemisphere. To determine the field of view, the size and orientation of the visual angle were determined according to methods comparable to those used on uloborids by Opell & Cushing (1986) and Opell & Ware (1987). Two deviations from these methods were employed. Measurements from frontal sections rather than sagittal sections were used and the tapetal periphery was taken to represent the limits of the visual cells and therefore define the width of the retina.

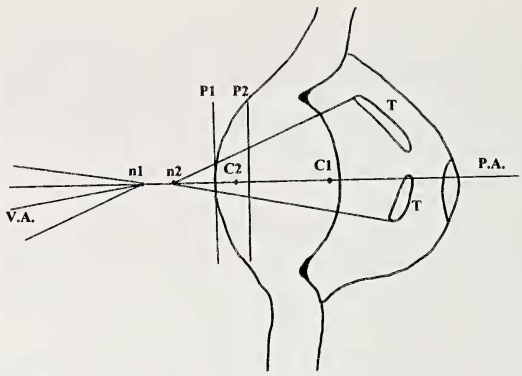


Figure 2.—Diagrammatic section of the secondary eye of B.insignis. n1 = front nodal point; n2 = rear nodal point; C1 = center of curvature of front of lens; C2 = center of curvature of the rear of lens; P1 = front principal plane; P2 = rear principal plane; P.A. = principal axis; T = tapetum; V.A. = visual axis.

Size of visual angle.—To ascertain the field of view of each eye, the angle at which light can enter to activate visual cells must be calculated; this is the visual angle. The visual angle of *B. insignis* was determined mathematically using measurements taken from sections of the eye (Fig. 2). A simple lens has two centers and two radii of curvature, one for both the front surface and the rear surface of the lens. The line joining the two centers is the principal axis of the lens. The refractive index of each lens was required to calculate the front and rear principal planes (Fig. 2), and was determined using measured focal length in conjunction with the radii of curvature of each lens (Table 1). This index was then used to calculate the principal planes (Table 1). The refractive index of air was assumed to be 1.00 and the refractive index of spider saline was assumed to be 1.33 (Land 1969). Drawings were made of each lens and its retinal hemisphere with the principal axis, principal planes and nodal points added to the reconstruction (Fig. 2). The rear nodal point was calculated by measuring the focal length forward from the retinal hemisphere along the principal axis. The front nodal point was then calculated since the distance between the front and

rear nodal points along the principal axis equates to the distance between the principal planes.

To determine the visual angle of each eye, sections from the frontal plane were used. Lines were drawn from the peripheral retinal cells in front of the tapetum to the rear nodal point and the angle these lines made with the principal axis was measured. An inverted projection of this angle from the front nodal point produced the eye's visual field (Fig. 2). A line bisecting this field represents the visual axis. To plot the visual field around the visual axis, the angle made with the principal axis was measured.

Orientation of visual angle.—To accurately plot visual fields, the relative positions of each eye must be known, therefore the principal axis must be determined relative to both its frontal and sagittal planes. The former was determined by placing the specimen under a dissecting microscope attached to a digital camera. A line was drawn to bisect the specimen along the midline. A second line was drawn along the points where the lens merged with the spider's carapace, through the widest part of the eye's ellipse. A third line was then drawn through the center of the eye and perpendicular to the second line drawn. The angle this line made with the midline of the carapace was recorded, and represented the eye's frontal orientation relative to the sagittal plane. To determine the eye's sagittal orientation, a similar method to above was employed in which the spider was placed on its side and a similar set of angles was created to measure the angle of the principal axis relative to the frontal plane.

Total visual arc, the angle of the principal plane and the visual angle were used to plot fields of view for *B. insignis* by moving the principal axis relative to the center of a geological stereonet accounting for the deviations from the sagittal and frontal planes. Visual fields were produced using the visual axis as a central point, around which the angle of the visual arc was plotted.

Uniformity of refractive index.—The refractive index of each lens was required to calculate the size of the visual angle. The methods used in this study to evaluate refractive index in *B. insignis* require that at least two specimens be used; one to determine the eye's focal length and one to determine the lens's physical properties. To reduce error that may result from using two specimens, mean measurements of focal length for each eye type were used, thereby accounting for possible differences in focal lengths between the two specimens.

Representative specimens from the study population have been deposited in the Western Australian Museum. Slide preparations are held in the Zoology Building, School of Animal Biology, University of Western Australia.

RESULTS

External ocular organization.—The eyes of *B. insignis* were widely spaced along the carapace but not deeply set (TEW = 36.69 ± 0.61, TED = 13.06 ± 0.42, n = 20). Diameters of the eyes are shown in Table 2. There was a significant difference in the sizes of the four different types of eyes for *B. insignis* ($F_{19,3}$ = 15.0, $P < 0.001$). The PL eyes were significantly larger than all others, while both pairs of anterior eyes and both pairs of medial eyes were similar in size.

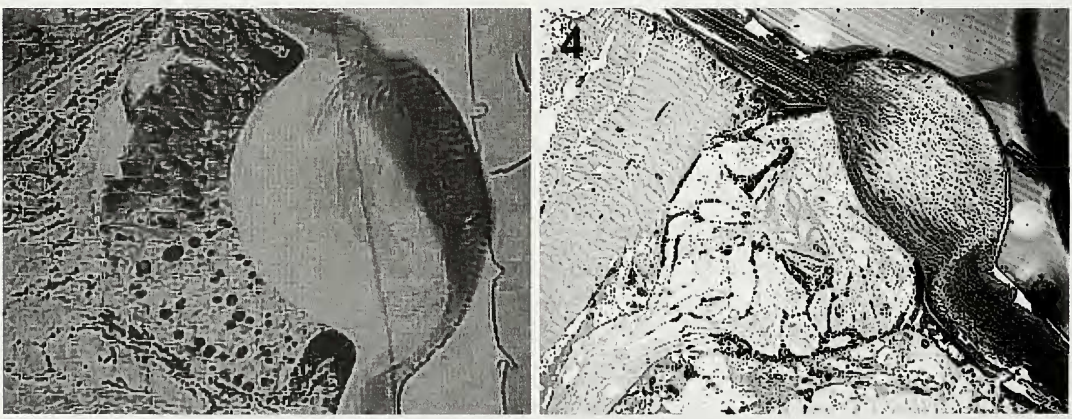
Internal ocular organization.—The AM eyes (Fig. 3) display a typical bi-convex lens formed by a visible thickening of the cuticular layer. The lens is separated from the retina by a layer of columnar vitreous cells. The retina is composed of visual cells and pigment cells. The most anterior portion of the visual cell, which contains the rhabdomeres, borders the vitreous layer and the nuclei lie below.

In the secondary eyes the boundary separating the rhabdomeres from the visual cells is marked by the tapetum. In *B. insignis*, a 'canoe-shape' tapetum, characteristic of most species in the amaurobioid clade (Homann 1971; Land 1985) was found (Fig. 4). The visual cells in these eyes bend around the tapetum, exiting through the opening between the adjacent tapetal plates. In the eyes of *B. insignis*, one discrete nerve bundle was found to emerge from each eye.

Resolution.—The optic nerves from all four pairs of eyes of *B. insignis* were found grouped together, surrounded by muscle along the midline of the prosoma. Identification of the eye from which each of the six nerve bundles originated, was possible by observing the arrival sequence (within the slides) of each nerve bundle and the direction from which it originated. The number of nerve axons (indicating resolution; Table 2) found in *B. insignis*

Table 1.—Equations used in histological methods.

Focal length (F):	
$F = \frac{i}{o}u$	i image length o object length u object and eye separation F focal length
Refractive index (n):	
$\frac{1}{F} = (n - 1)\left[\frac{1}{r_1} + \frac{1}{r_2} - \frac{d(n - 1)}{nr_1r_2}\right]$	n refractive index r_1 radius of outer curvature r_2 radius of inner curvature d lens thickness
Power of lens surface (P):	
Front: $P_1 = \frac{\Delta n}{r_1}$	Δn the difference in the refractive index of the front lens and air or the rear lens and the bodily fluids r_1 radius of outer curvature
Rear: $P_2 = \frac{\Delta n}{r_2}$	r_2 radius of inner curvature
Equivalent power (P_E):	
$P_E = P_1 + P_2 - \frac{d}{n}P_1P_2$	P_1 front surface power P_2 rear surface power d lens thickness n refractive index
Principal planes (VH):	
Front: $V_1H_1 = \frac{d}{n} \times \frac{P_2}{P_E}$	d lens thickness n refractive index P_1 front surface power P_2 rear surface power P_E equivalent power
Rear: $V_2H_2 = \frac{d}{n} \times \frac{P_1}{P_E}$	
Nodal points (N):	
Determined by plotting f-number (sensitivity):	N_1 front nodal point N_2 rear nodal point F focal length d pigment ring diameter
$f = \frac{F}{d}$	



Figures 3–4.—3. Primary eye of *B. insignis*; 4. Secondary eye of *B. insignis*.

Table 2.—Summary of parameters measured for eyes of *B. insignis*. Values shown are mean values ± standard error (where calculated). Values for resolution are the mean of the left and right eye.

Eye	Eye diameters (as % of carapace) $n = 20$	Resolution (# nerve axons) $n = 1$	Resolution (# nerve axons/ visual angle) $n = 1$	Focal Length (μm) $n = 2$	Sensitivity (1/*f*-number) $n = 1$
AM	4.78 ± 0.15	328	3.5	233.60 ± 17.74	0.86
AL	4.99 ± 0.16	96	3.1	209.26 ± 2.58	0.37
PM	4.31 ± 0.14	119	3.2	210.26 ± 7.68	0.46
PL	5.71 ± 0.21	102	4.3	198.06 ± 4.38	0.34

was greatest for the AM eyes, followed in order by the PL, PM, and AL eyes. To compare the density of visual cells the number of nerve axons was divided by the size of the visual angle. All eyes were similar in density, being slightly greater in the PL, followed in order by the AM, PM and AL eyes (Table 2). This suggests that the retinal cell number in the AM eyes only maintains the resolution of these eyes, given their larger visual angle, and does not increase their resolution.

Focal length.—The eyes of *B. insignis* displayed no significant differences in focal length ($F_{1,3} = 3.1$, $P = 0.191$; Table 2).

Sensitivity.—Calculated *f*-numbers for *B. insignis* were relatively high (demonstrating a low amount of sensitivity; Table 2). The highest sensitivity in *B. insignis* was found in the AM eyes, which showed a considerably lower *f*-number than all other eyes in this species. The remaining AL, PL, and PM eyes had similar low sensitivities (Table 2).

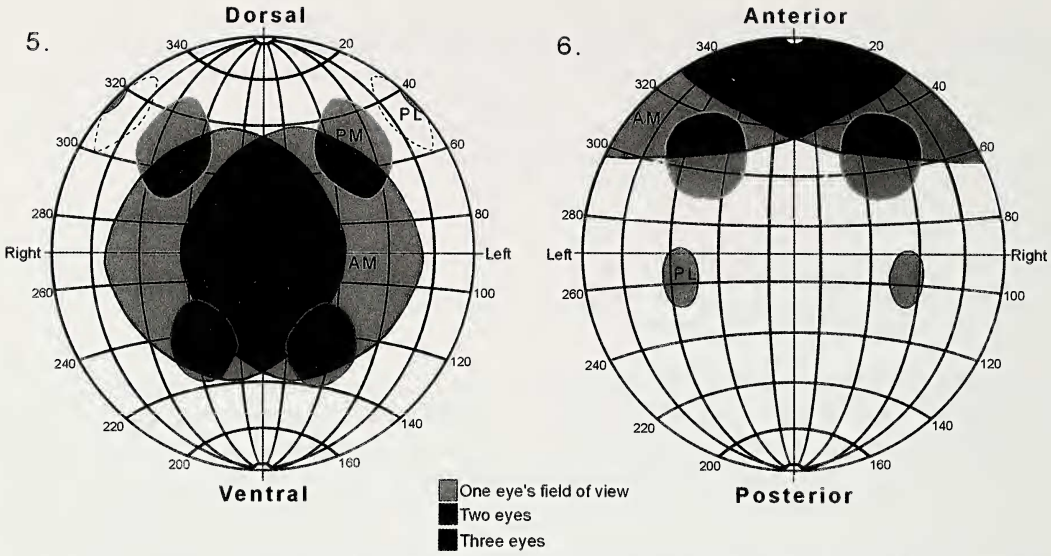
Field of view.—Table 3 provides values used to calculate the field of view for *B. insignis*. The AM eyes showed the greatest field of view, covering 130° along the horizontal meridian (Figs. 5 & 6). They also had a large degree of forward facing overlap, extending 55° above and below the horizontal, and having a maximum overlap of 66° on the horizontal meridian. Both sets of posterior eyes and the AL eyes have small visual fields (less than 40° horizontally or vertically) that show no overlap (Figs. 5 & 6). Both pairs of posterior eyes are directed 50° above horizontal, with the PM eyes directed anteriorly and the PL eyes laterally.

DISCUSSION

Badumna insignis has two rows of four eyes, reminiscent of a primitive external organization (Homann 1971), with all eyes showing little histological differentiation, or differences in diameter, resolution or focal length. The AM eyes were the most specialized, with the greatest sensitivity, the largest field of view and were the only eyes to display binocular overlap. None of the eyes of *B. insignis* displayed the long distance vision or resolution used for detecting prey at a distance.

However, there is a tradeoff between resolution and sensitivity due to physical restrictions of eye size (Blest & Land 1977). The visual system of *B. insignis* seems to be selected for sensitivity rather than resolution, as the resolution is low, even for web-building spiders. The orb weaver *Argiope amoena* (L. Koch 1878) typically has 400–500 optical nerve axons exiting the AM eyes (Uehara et al. 1977), which is greater than the resolution found in *B. insignis*.

The sensitivity of the secondary eyes in *B. insignis* (2.16–2.97) is far less than that of the nocturnally active web building uloborids, whose *f*-number ranges from 0.88–1.70 (Opell & Ware 1987). Instead, they more closely reflect those of the visually hunting diurnal jumping spiders, which have *f*-numbers ranging from 2.68–5.90 (Foelix 1982; Land 1969). This suggests that *B. insignis* utilize their secondary eyes under higher light levels. *Badumna insignis* is occasionally active during the day (Henderson & Elgar 1999) thus, the secondary eyes may be utilized during these periods. Conversely the *f*-number of the AM eyes of *B. insignis* resembles that of the nocturnal uloborids and appears more suitable for its typical nocturnal habit. This combination of sensitivities may allow *B. insignis* to be a more versatile hunter, predominately active in low light-levels, but capable of taking advantage of occasional daylight opportunities.



Figures 5–6.—Fields of view for *B. insignis*: 5. Anterior view; 6. Dorsal view. AM = anterior median eyes; AL = anterior lateral eyes; PM = posterior median eyes; PL = posterior lateral.

However, the lack of binocular vision displayed by any of the secondary eyes would restrict depth perception and therefore limit the use of these eyes in prey capture. The possible function of the secondary eyes remains unclear. With such small fields of view it is unlikely they would be useful in prey detection. These secondary eyes may be used for distinguishing light levels to control circadian rhythms (Uehara et al. 1994), or act simply as wide angle detectors of movement. Conversely, the AM eyes with their large forward facing fields of view and large area of binocular vision, would play an important role in recognition and judgement of distance to the entangled prey.

The web increases the perceptive area of a spider (Peters & Pfreundt 1986) and evidence suggests spiders can determine the identity of an object in the web by the vibrations it creates (Suter 1978; Barth 1982; Masters et al. 1986; Herberstein *et al.* 1998). Coupled with its poor visual acuity, this suggests that *B. insignis* relies on its web rather than its eyes for prey detection. The web of *B. insignis* also acts to entangle and ensnare prey, and so also plays a significant role in prey capture.

The relatively unspecialized visual system

Table 3.—Ocular properties and measurements used to calculate and plot fields of view for *Badumna insignis*.

Eye	Lens thickness (μm)	Radius of curvature (r1/r2, μm)	Refractive index	Pigment ring diameter (μm)	*f*-number	Total visual angle	Visual axis from physical axis	Visual axis from frontal plane	Visual axis from sagittal plane
AM	184.7	142.7/107.8	1.31	200.8	1.16	93°	8° right of right eye	0°	9°
AL	129.0	126.9/108.2	1.32	87.4	2.67	32°	6° right of right eye	33° ventral	20°
PM	109.4	108.3/98.5	1.28	97.5	2.16	37°	19° right of right eye	38° dorsal	33°
PL	91.5	112.3/97.8	1.29	33.3	2.97	24°	1° right of right eye	44° dorsal	90°

of *B. insignis* may be attributed to the utilization of the web. As well as functioning to ensnare prey, a web can also be protective. A complete field of view is not essential as the web warns the spider of some potential threats and provides a hidden retreat. The web essentially functions to increase the perceptive area for prey capture and may act in place of a highly developed visual system. However, *B. insignis* still requires a system for recognizing whether an object within the web is predator or prey. The araneophagic spider *Lampona cylindrata* (L. Koch 1866) (Araneae Lamponidae) is commonly known to prey upon *Badumna insignis* (Hickman 1967; Main, pers obs). The eyes of *B. insignis* appear adapted for close range recognition, due to the short-range focus and good depth perception of the AM eyes. Thus the visual system operates to inform *B. insignis* of the distance to an object and whether to attack or retreat.

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